Ann. For. Res. 67(2): 17-30, 2024
https://doi.org/10.15287/afr.2024.3482

ANNALS OF FOREST RESEARCH
www.afrjournal.org

Long-term persistence of butterfly diversity in a sustainably managed forest ecosystem

Thomas Schmitt[1,2]✉, Tobias Hennige[1,3], Alexej Maseluk[4], Jan Christian Habel[5]

Schmitt T., Hennige T., Maseluk A., Habel J.C., 2024. Long-term persistence of butterfly diversity in a sustainably managed forest ecosystem. Ann. For. Res. 67(2): 17-30.

Abstract In recent decades, intensification in land use has led to severe losses of biodiversity across major parts of the world. Studies from Central Europe revealed severe decline of insect diversity across agro-environments, but to a lower extent in forest ecosystems. Sedentary specialist species are suffering particularly, while mobile generalist species are much less affected. Numerous species are also disappearing from nature reserves. On the long run, biodiversity presumably can only be maintained in ecosystems of sufficient size, but is lost in small and isolated habitats. In order to test this assumption, we conducted butterfly counts over a period of 20 years in a large, heterogeneous and sustainably used forest ecosystem in southern Germany. We found no significant changes in diversity and abundance over the two decades of study. However, our data revealed a significant shift in species´ community structure over time, with the proportion of generalist species increasing and the proportion of specialist species decreasing. These changes are most likely due to changes in habitat structures. At the beginning of our study, wind-blows resulting from the heavy storms in the late 1990s represented open areas, but subsequently reforested in the wake of natural succession. Since these temporary open habitats had attracted a particularly high number of specialised species, the observed changes are probably due to these natural processes in a forest ecosystem. In general, our results show that heterogeneous ecosystems of large size may preserve a species-rich butterfly community in the long run.

Keywords: insect decline, biodiversity loss, habitat size, habitat quality, time-area counts, ecological traits

Addresses: [1]Senckenberg German Entomological Institute, Müncheberg, Germany | [2]Entomology and Biogeography, Institute of Biochemistry and Biology, Faculty of Science, University Potsdam, Potsdam, Germany | [3] University of Tuebingen, Institute of Evolution and Ecology, Tübingen, Germany | [4]Nuertingen-Geislingen University, Fakultät Umwelt Gestaltung Therapie, Nürtingen, Germany | [5]Evolutionary Zoology, Department of Environment and Biodiversity, Paris Lodron University Salzburg, Salzburg, Austria.

✉ **Corresponding Author:** Thomas Schmitt (thomas.schmitt@senckenberg.de).

Manuscript: received January, 25, 2024; revised October 8, 2024; accepted October 12, 2024.

Introduction

Intensification of agriculture has led to dramatic losses in species diversity across the globe (Raven & Wagner 2021, Rumohr et al. 2023). Long-term observations have shown a strong decline in insect diversity for Europe, but also a rapid decrease in species abundances and biomass of flying insects (Hallmann et al. 2017, 2021; Cardoso et al. 2020). These trends have negative effects on organisms that depend on insects as food source, such as birds and bats (Møller 2019, Bowler et al. 2019). However, not only species diversity, abundance and biomass of insects has decreased strongly, but also community compositions. For example, remarkable changes in community composition have been observed over the last decades, towards homogeneous communities dominated by some few generalist species (Olden 2006, Habel et al. 2019a, Bonelli et al. 2022, Ternisien et al. 2023). In parallel, sedentary and ecologically specialised species are disappearing rapidly, as these respond highly sensitive to environmental changes (Habel et al. 2016, Ternisien et al. 2023).

A main driver causing these losses in diversity and the homogenisation in species composition are destructions of species-rich habitats, such as peatlands, natural and light forests, wet meadows and calcareous grasslands (Thomas 2016). However, in addition to the vanishing of these habitats, the decrease of habitat quality also has negative effects on biodiversity (Thomas 2016). For example, the influx of nitrogen causes the vanishing of numerous plant species, and hence shifts in the composition of plant species and habitat structures (Lin et al. 2021). These changes are leading to modifications in microhabitat structures, including microclimate (Habel et al. 2016). In addition, pesticides spread across landscapes by drift and even accumulate in nature reserves, mostly depending on topographical structures and thermal conditions in a landscape (Huemer & Tarmann 2001). In consequence, the reduction of habitat quality is assumed to be the main driver causing recent biodiversity loss across Central Europe (Thomas 2016). The mentioned processes act at the landscape level. Therefore, it is not surprising that biodiversity decline can also be observed at sites that have not undergone any intensification (Seibold et al. 2019), and even in nature reserves (Habel et al. 2016).

However, this decline in species diversity and the change in species composition seems to be much more pronounced in small and geographically isolated habitats (in the agro-environment) if compared to large and still mostly continuous habitats (as is still often the case within forested areas) (Seibold et al. 2019). Thus, stochastic processes (such as demographic fluctuations) have a much stronger impact in habitats with populations composed of some few individuals than in large habitats, which offer space for large population networks, an important precondition for higher species persistence (Melbourne & Hastings 2008). In addition, the influx of pesticides is partly retained in larger ecosystems. It becomes buffered by the vegetation structure of a forest, and thus cannot diminish habitat quality and weaken populations as much as frequently observed in open landscapes (Müller et al. 2018). In conclusion, biodiversity can be maintained much more efficiently in a large habitat than in numerous small remnants.

However, even semi-natural ecosystems, such as many European forests, might be subject to large cyclic changes in their habitat structures (Pickett & White 1985). In particular, natural disasters, such as heavy storms or wildfires, shape ecosystems and represent a starting point for natural succession (Walker & Del Moral 2003). Frequently, such disturbances are essential to create open spaces and thus to get light into an ecosystem, which enhances biodiversity significantly (Sparks et al. 1996, Anthes et al. 2008). In particular, the interplay of ephemeral and permanent as well as natural and anthropogenic open spaces is of high relevance for the dynamics of biodiversity, as frequently found in forests.

The Oettinger Forest in Franconia (southern Germany) represents a large and sustainably used forest ecosystem. It provides many open habitats (meadows, forest clearings, abandoned quarries, sand pits), located inside the forest, but also along the forest margins (Schmitt 2003). The forested area extends over approximately 40 km^2 and is home of various ecologically specialised butterfly and burnet moth species such as *Cupido minimus*, *Fabriciana adippe*, *Boloria euphrosyne*, *Limenitis camilla* and *Zygaena trifolii* (Schmitt 2003). Due to the strong storms at the end of the 1990s, large wind-blows existed in 2001, remarkably enlarging the open space. We repeatedly assessed butterflies on defined sampling plots spread across the forest ecosystem, representing all major habitat types. We also recorded habitat parameters, and classified each butterfly species according to its ecology. Based on the data collected, we analyse changes in butterfly diversity and shifts in community composition. In particular, we wish to understand the influence of sustainable use on the butterfly communities of a forest and the impact of severe disturbance like strong storm events. We hypothesise that both have positive effects on butterfly species richness. Therefore, we address the following specific research questions:

1. Are butterfly diversity and species community structures maintained in the studied forest ecosystem over the two decades studied?
2. Do ecologically specialised species persist in the studied forest ecosystem?
3. What is the importance of open structures in the forest for maintaining the diversity of butterflies?
4. What are the effects of large-scale wind-blows and subsequent reforestation on the development of butterfly populations?

Materials and Methods

Study area

The forest ecosystem Oettinger Forest is located in Franconia, southern Germany (49°00’ N; 10°30’ E) (Fig. 1), ranging from 425–545 m a.s.l. and covering about 40 km^2. It is surrounded by agricultural land and consists of spruce (*Picea abies*) (38%), beech (*Fagus sylvatica*) (26%), oak (mostly *Quercus petraea*) (10%), and other deciduous and conifer tree species (such as lime (*Tilia cordata*), alder (*Alnus glutinosa*), pine (*Pinus sylvestris*) and fir (*Abies alba*)). The forest has a long tradition of sustainable forestry and its management is according the Programme for the Endorsement of Forest Certification Scheme (PEFC). Logging is usually carried out in the form of small clear-cuts. Due to the long period of forest management, all different age classes of trees are present, often in small plots of age class forests of the same species, but mixed forests also exist. However, very old trees (i.e. >150 years) are rare. The heavy storms of the late 1990s caused large wind-blows, which have since developed back into young forests. As a result, the forest has been subject to significant dynamics over the study period.

Three types of meadows exist in the area, hay meadows (grass and herbs are cut and removed), mulched meadows (vegetation cover is cut but remains on the meadow for decomposition and fertilisation), and hunting meadows (planted meadows with Poaceae, Brassicaceae or Fabaceae crops, mown or mulched once to twice a year). Furthermore, several fish ponds, swamps and abandoned quarries and sand pits exist scattered throughout the forest. Gravel roads transgress the forest and are often accompanied by wide strips (2-3 m) of herbaceous plants (thistles, nettles) and are mown only occasionally.

Study design

We selected 41 sampling plots (size: 0.2-2.2 ha; mean: 1.13 ha) across the forest ecosystem of which 37 were sampled in all three years; the remaining four plots were not sampled in one year each, i.e. plot 10 not in 2021, plots Z1-Z3 not in 2001 (Figure 1).

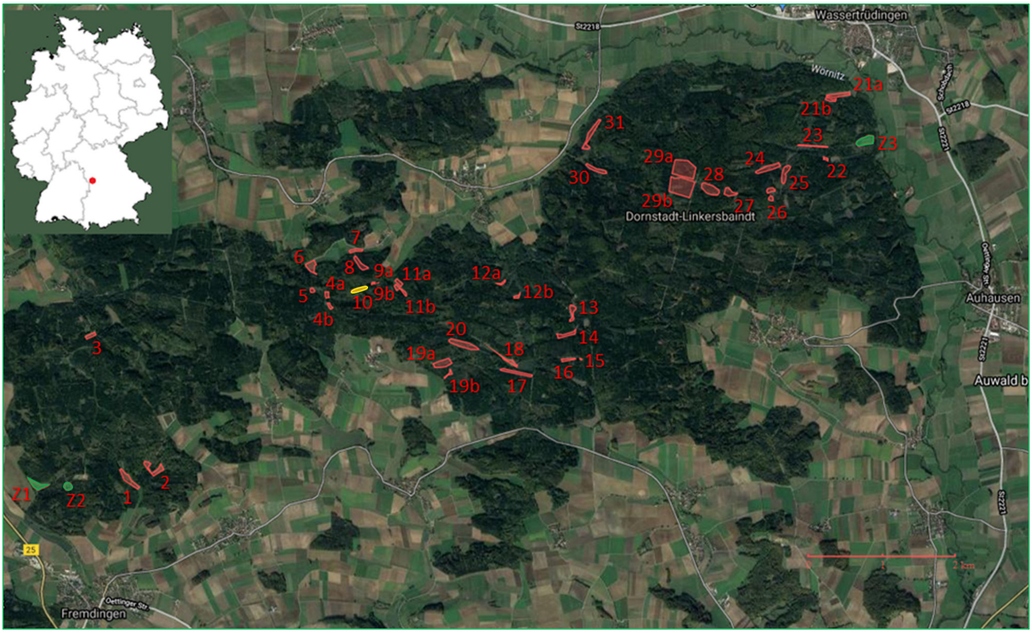

Figure 1 The Oettinger Forest in southern Germany (red dot in small inlet map) with the 41 sampling plots marked in red (counting all years), yellow (counting in 2001 and 2019) and green (counting in 2019 and 2021) distributed over 40 km^2.

The plots represent the different main habitat types occurring in the forest ecosystem. The individual plots were at least 200 m apart. In 2001, 13 plots were wind-blows, six forests (coniferous, mixed, and deciduous), 15 meadows, three queries, and one sand pit. 11 out of the 13 wind-blows were regrown by young trees and thus turned into typical forest plots over the 20 years. To still have a certain number of such open plots, we added two clearing plots during the 2019 and 2021 assessments for also representing this type of habitat appropriately. Two of the queries and the sand pit were still open in 2001 but mostly overgrown by bushes and young trees in 2019 and 2021. As one of the meadow plots was inaccessible during the 2021 assessment, we added one meadow plot to maintain the number of this plot type constant.

Collection of data

From May to August, butterfly counts were conducted from 10 am to 5 pm under suitable weather conditions (≥18°C, sunny, little or no wind). All sampling sites were visited five (in 2001) or seven times (2019, 2021), for 20 minutes per plot and visit. During this time, one observer slowly and randomly walked across the plot, counting all butterfly and burnet moth individuals (hereafter simply called butterflies) by direct observation (flying and resting) within a 5 m radius. This technique yields similarly reliable results as line transect counts, but mostly reflects better the true number of species that is more strongly underestimated by line transects (Kadlec et al. 2012, Kral-O'Brien et al. 2021, Suman et al. 2021, Barkmann et al. 2023).

The timing of visits was randomised so that each plot was visited at different times. If more than ten individuals of one species were present at a plot, we estimated the number of individuals. We did not consider larval stages. The majority of species can be identified if resting or even flying. In case an individual could not be undoubtedly assigned to a species, it was caught with a butterfly net and identified. *Leptidea sinapis* and L. *juvernica* as well as *Zygaena purpuralis* and *Z. minos* were considered as species complexes, as a morphological distinction is not possible in the field. Nomenclature and order in Table 1 follow the checklist of Wiemers et al. (2018). The authors and years of first description are also given in this table and, for means of readability, not when a species is first mentioned in the text.

Field work was performed by TS in 2001, AM in 2019, and TH in 2021. TS is a butterfly specialist, the Master students AM and TH were intensively trained before the respective field work season and constantly supported during field work by TS, in particular in the determination of difficult species. Therefore, they were able to collect data reliably.

Statistics

Dominance structures were built with six categories: >32.0% eudominant, 10.0–31.9% dominant, 3.2–9.9% sub-dominant, 1.0–3.1% resident, 0.32–0.99% sub-resident, <0.32% sporadically. Dominance structures were constructed for each year and within the habitat types for each year.

We calculated the following diversity indices: Shannon index (H), calculated on the basis of the natural logarithm, Evenness (EH) derived from this index, Simpson index (D) reflecting the probability of randomly finding two individuals of the same species in a population, presented in its reversed form 1-D, Fisher's alpha index (S) as a logarithmic series model. Chao 1 and ACE were applied to estimate the amount of species in each plot. For means of comparability, indices were calculated using the results of five sampling campaigns per year; therefore, campaign 2 and 7 were discarded for 2019 and 2021 to best fit the three years. To test for differences among indices among years, repeated-measures Kruskal-Wallis tests (below for means of simplicity KW tests) were carried out, followed by two-sided paired Tukey's tests for *a posteriori* assessment. These analyses were performed with data from all permanent plots, and with data from only the plots that did not change their habitat type over the study period.

Cochran-Q tests allow analysing the plot occupation of different species along the sampling years. If species showed significant changes in plot occupancy from one year to another, it was afterwards analysed by a paired McNemar Post-Hoc test.

We performed non-metric multidimensional scaling (NMDS) and 2-D canonical correspondence analyses (CCA) with habitat types as cofactors for all years and for each single year to get information about clustering of community composition in different habitat groups within and among years. Ten co-factors (Forest: coniferous, deciduous, mixed; Meadow: mulched, hay, game; Clearing; Other habitat types) were added. Prior to analyses, sampling data were transformed applying the natural logarithm to reduce the impact of the most common species. Convex hulls were added to all ordinations. Further settings were retained by default.

Based on ecological characteristics suggested by Bink (1992), nine trait categories were adapted to our data set, i.e. habitat specificity (one habitat or habitat complex vs. several); phagy of caterpillars (monophagous – one genus, oligophagous – one family, polyphagous – more than one family); egg laying specificity (nine categories: highly specific to random); heat resistance (three categories: low – intermediate – high); cold resistance (three categories: low – intermediate – high); dispersal capacity (nine categories: very sedentary to true migrant species); necessary habitat size (nine categories: 1 ha to > 200 km^2), population density (nine categories: 2/km^2 to 1000/ha); r/K strategy (1 = true K to 4 = true r). Trait values were added for *Zygaena* species using Ebert et al. (1994), and expertise of TS. All data are given in Sheet S1. Means for each trait in each plot per year were calculated based on the real count numbers of individuals, presence/absence and ln transformed values; only data from permanent plots entered the analyses. To test for changes among sampling years, paired Wilcoxon tests were performed. Differences among the four habitat types within each year were examined with Mann-Whitney U-tests. Eleven clearing plots from 2001 changed their habit type to forest over the years, making them unsuitable for paired analyses within habitat types among years. To avoid type 1 errors, the Benjamini & Hochberg (1995) procedure was performed. All statistical analyses were performed using PAST version 4.07b (Hammer et al. 2001).

Results

During the three sampling years, we counted 19,509 butterflies and burnet moths (hereafter called butterflies for means of simplicity), representing 56 species.

In total, we performed 19 sampling campaigns (5 in 2001; 7 in 2019 and 2021, each) on 38 (2001), 41 (2019) and 40 plots (Table 1; Table S1; row data Sheet S2). 34 species (i.e. 61%) were recorded in all three years.

Table 1 Total butterfly individuals (Ind) per year and mean per transect walk (trw) on all transects recorded in the Oettinger Forest during all three years, i.e. excluding transects 10, Z1, Z2 and Z3.

	2001		2019		2021	
	Ind	Ind/trw	Ind	Ind/trw	Ind	Ind/trw
Papilionidae						
Papilio machaon Linnaeus, 1758	17	0.092	0	0	0	0
Hesperiidae						
Carterocephalus palaemon (Pallas, 1771)	79	0.427	13	0.050	46	0.178
Ochlodes sylvanus (Esper, 1778)	343	1.854	38	0.147	280	1.081
Thymelicus sylvestris (Poda, 1761)	180	0.973	33	0.127	32	0.124
Thymelicus lineola (Ochsenheimer, 1808)	9	0.049	29	0.112	109	0.421
Pyrgus malvae (Linnaeus, 1758)	51	0.276	1	0.004	1	0.004
Pieridae						
Leptidea sinapis (Linnaeus, 1758) / juvernica Williams 1946	109	0.589	32	0.124	64	0.247
Gonepteryx rhamni (Linnaeus, 1758)	255	1.378	349	1.347	796	3.073
Colias hyale (Linnaeus, 1758)	3	0.016	4	0.015	1	0.004
Aporia crataegi (Linnaeus, 1758)	0	0	0	0	1	0.004
Pieris brassicae (Linnaeus, 1758)	23	0.124	26	0.100	43	0.166
Pieris rapae (Linnaeus, 1758)	136	0.735	185	0.714	227	0.876
Pieris napi (Linnaeus, 1758)	910	4.919	501	1.934	1064	4.108
Anthocharis cardamines (Linnaeus, 1758)	98	0.530	9	0.035	53	0.205
Lycaenidae						
Lycaena phlaeas (Linnaeus, 1761)	12	0.065	36	0.139	17	0.066
Thecla betulae (Linnaeus, 1758)	0	0	0	0	1	0.004
Favonius quercus (Linnaeus, 1758)	0	0	1	0.004	0	0
Callophrys rubi (Linnaeus, 1758)	1	0.005	3	0.012	9	0.035
Satyrium w-album (Knoch, 1782)	0	0	0	0	2	0.008
Celastrina argiolus (Linnaeus, 1758)	11	0.059	8	0.031	40	0.154
Phengaris nausithous (Bergsträsser, 1779)	0	0	1	0.004	0	0
Cupido argiades (Pallas, 1771)	0	0	18	0.069	5	0.019
Cupido minimus (Füssly, 1775)	33	0.178	0	0	0	0
Cyaniris semiargus (Rottemburg, 1775)	0	0	0	0	3	0.012
Aricia agestis (Dennis & Schiffermüller, 1775)	1	0.005	0	0	0	0
Polyommatus icarus (Rottemburg, 1758)	42	0.227	55	0.212	60	0.232
Nymphalidae						
Limenitis camilla (Linneaus, 1764)	4	0.022	0	0	0	0
Issoria lathonia (Linnaeus, 1758)	3	0.016	13	0.050	0	0
Brenthis ino (Rottemburg, 1775)	2	0.011	0	0	0	0
Argynnis paphia (Linnaeus, 1758)	44	0.238	265	1.023	909	3.510

Fabriciana adippe (Dennis & Schiffermüller, 1775)	58	0.314	80	0.309	115	0.444
Boloria selene (Dennis & Schiffermüller, 1775)	97	0.524	19	0.073	25	0.097
Boloria euphrosyne (Linnaeus, 1758)	2	0.011	5	0.019	15	0.058
Boloria dia (Linnaeus, 1758)	13	0.070	0	0	1	0.004
Apatura ilia (Dennis & Schiffermüller, 1775)	1	0.005	0	0	1	0.004
Apatura iris (Linnaeus, 1758)	2	0.011	0	0	0	0
Araschnia levana (Linnaeus, 1758)	249	1.346	38	0.147	1007	3.888
Vanessa cardui (Linnaeus, 1758)	37	0.200	70	0.270	19	0.073
Vanessa atalanta (Linnaeus, 1758)	44	0.238	25	0.097	84	0.324
Aglais io (Linnaeus, 1758)	440	2.378	26	0.100	829	3.201
Aglais urticae (Linnaeus, 1758)	17	0.092	9	0.035	11	0.042
Polygonia c-album (Linnaeus, 1758)	35	0.189	13	0.050	89	0.344
Melitaea diamina (Lang, 1789)	0	0	13	0.050	0	0
Melitaea athalia (Rottemburg, 1775)	1	0.005	1	0.004	0	0
Coenonympha pamphilus (Linnaeus, 1758)	71	0.384	68	0.263	191	0.737
Coenonympha arcania (Linnaeus, 1761)	6	0.032	0	0	0	0
Pararge aegeria (Linnaeus, 1758)	153	0.827	7	0.027	59	0.228
Lasiommata megera (Linnaeus, 1767)	0	0	0	0	22	0.085
Melanargia galathea (Linnaeus, 1758)	26	0.141	96	0.371	437	1.687
Aphantopus hyperantus (Linnaeus, 1758)	825	4.459	303	1.170	759	2.931
Maniola jurtina (Linnaeus, 1758)	331	1.789	671	2.591	1886	7.282
Zygaenidae						
Zygaena purpuralis (Brünnich, 1763) / minos (Dennis & Schiffermüller, 1775)	4	0.022	0	0	0	0
Zygaena osterodensis Reiss, 1921	0	0	0	0	6	0.023
Zygaena viciae (Dennis & Schiffermüller, 1775)	17	0.092	1	0.004	79	0.305
Zygaena filipendulae (Linnaeus, 1758)	8	0.043	4	0.015	147	0.568
Zygaena trifolii (Esper, 1783)	2	0.011	0	0	0	0

The number of species did not differ remarkably among years (46; 41; 44). However, the number of individuals recorded varied strongly (5014; 3648; 10,847), even if correcting for the number of campaigns and plots (per campaign: 1056; 508; 1550; adjusted to 40 plots). 15 species were exclusively observed during one single year; eight of them in 2001 (*A. iris*, *A. agestis*, *B. ino*, *C. arcania*, *C. minimus*, *L. camilla*, *Z. purpuralis/minos*, *Z. trifolii*), two in 2019 (*F. quercus*, *Ph. nausithous*), and five in 2021 (*A. crataegi*, *C. semiargus*, *S. w-album*, *Th. betulae*, *Z. osterodensis*). Three species were only missing in 2001 (i.e. *C. argiades*, *L. megera*, *M. diamina*), two in 2019 (*A. ilia*, *P. machaon*), and two in 2021 (*I. lathonia*, *M. athalia*); Tables 1 and S1, with Table 1 also giving the author and year of first description. Excluding the three supplementary plots, *B. dia* (in 2019), *M. diamina* (in 2021), and *P. machaon* (in 2021) were not detected in the respective year.

Dominance structures differed remarkably between 2001 on the one hand and 2019 and 2021 on the other (Fig. S1), and the number of dominant species increased with time. Thus, only *P. napi* (19%) and *A. hyperantus* (18%) were dominant in 2001, while it was *M. jurtina* (24%), *P. napi* (16%), *G. rhamni* (11%) and *A. hyperantus* (10%) in 2019, as well as *P. napi* (22%), *M. jurtina* (21 %) and *A. levana* (10%) in 2021. Similar changes were observed in all four habitat types separately (Fig. S2).

Based on five yearly campaigns (i.e. excluding data of campaigns 2 and 7 for 2019 and 2021), 35 species (with a total N ≥ 10 on the 37 constantly assayed plots) were recorded in 2001 and in at least one of the years 2019 and 2021. Of these, 19 and 12 species showed a decrease to half of the abundance from 2001 to 2019 and 2021, respectively; an increase to more than twice the number of individuals was observed for six (2019) and 11 species (2021); see Table S2. Cochran Q test returned significant changes in plot occupation among the years for 21 species. Consistent significant loss of occupied plots since 2001 was obtained for one species (*P. malvae*), while five species showed a consistent increase (*Th. lineola*, *P. rapae*, *A. paphia*, *M. jurtina*, *M. galathea*), see Table S3.

At the plot level, the means of several biodiversity indices differed significantly among years, i.e. species numbers (KW test, p<0.0001), number of individuals (KW test, p<0.0001), Evenness (KW test, p=0.002), Chao 1 (KW test, p=0.008), and ACE (KW test, p=0.0005), but not Shannon (KW test, p=0.065), Simpson (1-D) (KW test, p=0.335), and Alpha (KW test, p=0.221). Numbers of species and individual differed significantly between all pairs of years (two-sided paired Tukey's test). Evenness differed significantly between 2001 and the two other sampling years. Comparing Chao 1 and ACE revealed no significance between the years 2001 and 2021, but 2019 had significantly smaller values than these (Fig. 2).

More than half (55%, i.e. 31 species) of the 56 species were observed in all four habitat types. Six only were recorded on meadows (*A. ilia*, *B. ino*, *F. quercus*, *Ph. nausithous*, *C. semiargus*, *Th. betulae*), one only in forests (*A. crataegi*), two only in the other habitat types like quarries and sandpit (*C. minimus*, *Z. osterodensis*), and one only on clearings (*A. agestis*). The number of species observed in all habitat types increased significantly with time (i.e. 12 species, 26% in 2001; 18 species, 44% in 2019; 28 species, 64% in 2021; KW test, p<0.0001; all Tukey's tests, p<0.02) (Fig. 3; details: Sheet S4). NMDS well separated the three years. Analysing all years separately, a large community overlap was observed among all four habitat types. Only in 2001, the community of the forest habitat type was well distinguished from all others (Fig. 4).

Trait changes in the entire community along years were analysed on the basis of all continuously analysed plots (KW tests with

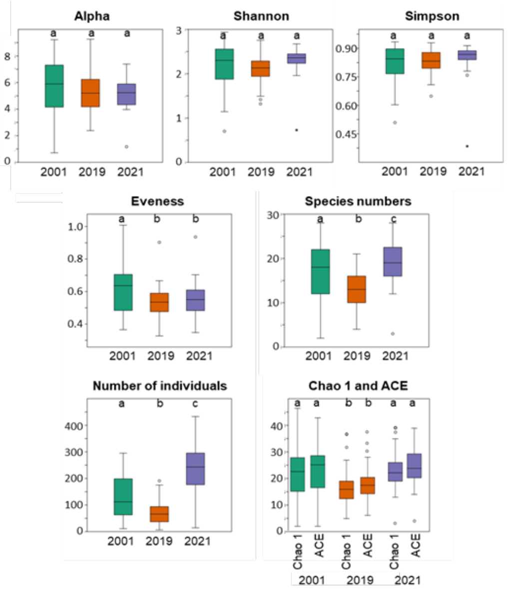

Figure 2 Box plots with standard deviations for mean values of Alpha, Shannon, Simpson (1-D), Evenness, species diversity, number of individuals, as well as the two estimators Chao 1 and ACE for the three years 2001 (green), 2019 (red) and 2021 (blue). Different letters indicate significant differences.

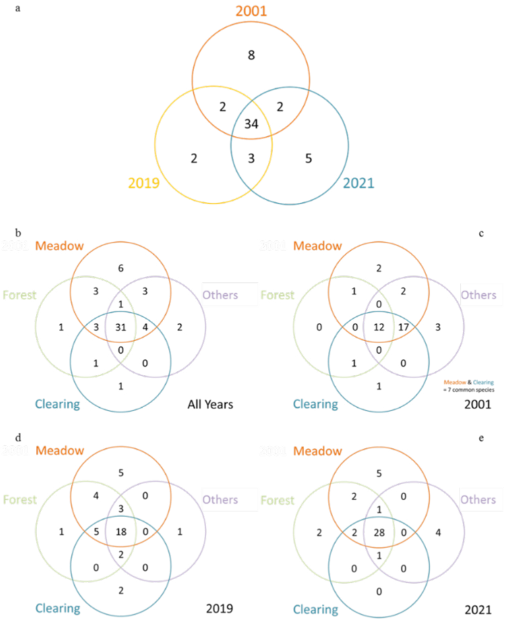

Figure 3 Distribution of the 56 butterfly and burnet moth species in the Oettinger Forest over the years 2001, 2019, and 2021 (a) as well as the habitat types meadow, forest, clearing, and others (b-e).

subsequent Tukey's tests). Five of the nine examined traits showed significant results. Communities in 2019 and 2021 required larger habitats, were more specific about their larval food plants, more heat resistant and tended to populations with higher densities than in 2001 (Sheet S3 and S4). Differences of traits among habitat types within one sampling years (tested by Mann-Whitney U-tests followed by Benjamini & Hochberg (1995) procedure), were only obtained in 2001, i.e. seven p-values were significant. Differences within the same habitat type among sampling years (based on plots that did not change their habitat characterisation over the years; paired Wilkoxon tests followed by Benjamini & Hochberg (1995) procedure) revealed a number of significant differences for meadows and forests. Due to insufficient numbers of cases, clearings partly had to be excluded from this analysis.

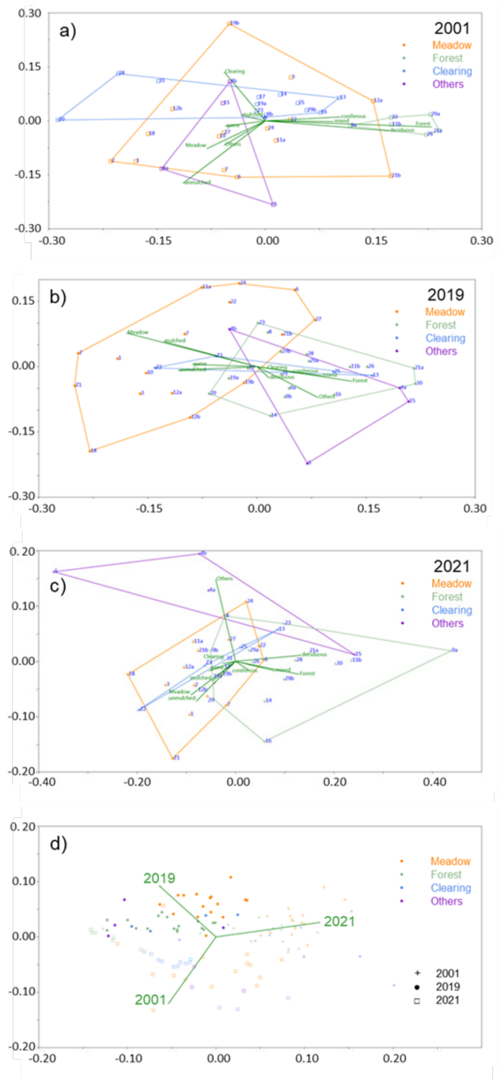

Figure 4 NMDS analyses for the three study years, and for all years combined. All plots were grouped to either meadow (orange), forest (green), clearing (blue) or others (purple). Groups and subgroups for meadow (i.e. mulched, hay, others) and forest (i.e. coniferous, deciduous, mixed) are visualized due to the triplot length and direction (a-c). In (d), the three cofactors represent the sampling years. Squares stand for 2001, dots for 2019 and, crosses for 2021.

Discussion

Species richness and abundance

The overall diversity of butterflies and burnet moths in the Oettinger Forest ecosystem has remained largely constant over the study period. While a strong decline in butterfly diversity (van Dyck et al. 2009, Habel et al. 2019b, 2022; Sánchez-Bayo & Wyckhuys 2019, Warren et al. 2021) and a general loss of insects (Hallmann et al. 2017, Habel et al. 2019a) has been recorded in open, agriculturally used areas of Central Europe over the last decades, this trend seems to be less pronounced in forest ecosystems. Thus, the extensive study by Seibold et al. (2019) showed that negative trends in insect populations (species number, diversity, abundance and biomass) are less pronounced in forests than in open agro-environments. For the latter, multiple factors impact habitat quality and habitat configuration and subsequently drive these losses. Hence, most of the remaining semi-natural habitats in agricultural landscapes are comparatively small and often geographically isolated from each other. This accelerates the impact of negative edge effects and subsequently leads to reduced persistence of local populations (Dennis & Eales 1997). As a result, stochastic effects that can evoke local extinctions have a particularly strong and frequent impact (Melbroune & Hastings 2008). This is aggravated by the fact that re-colonisations from neighbouring habitats hardly ever take place (Thomas 2016).

In contrast to semi-natural habitats in open agricultural landscapes, forest ecosystems in most cases are geographically much larger. Furthermore, numerous semi-natural areas do exist, even in a forest used for forestry, especially if the forest ecosystem is a mosaic of habitats (Viljur & Teder 2015), as in case of the Oettinger Forest. Thus, larger populations and even entire population networks can establish in such forest ecosystems. As a result, populations of many forest species have a significantly higher persistence than species of open agro-environments (Habel et al. 2019a, b). Therefore, species diversity is more likely to be maintained in forests in the medium term – as shown in our example. In addition, pesticides are used significantly more in agricultural landscapes than in forests, and nitrogen compounds are also released significantly less in the latter. In addition, both are drifting much more efficiently in open landscapes and accumulate in habitats such as meadows. This strongly impairs habitat quality, especially in semi-natural areas of open land. In contrast, such substances and additional negative edge effects are partly detained by forest margin trees (Ganuza et al. 2022). Consequently, populations in forest ecosystems should be better protected from them than comparable occurrences in the open countryside.

In contrast to the stable species diversity over 20 years, our results revealed strong abundance fluctuations among the three study years, differing for the individual species. Thus, abundances across all plots and species showed a marked increase from 2001 to 2021, but at the same time very low values in 2019. Numerous studies on the dynamics of insect abundances confirm such strong fluctuations, even over such short periods of time (e.g. between single consecutive years) (Hausmann et al. 2022). Such pronounced fluctuations are usually driven by environmental factors, such as weather or the mass occurrence of antagonists (such as parasitoides) (Harrison et al. 2015, Mills et al. 2017). Furthermore, there was a large increase in some few species, such as *V. cardui* in 2019; in parallel, most other butterfly species had rather low population sizes compared to the other two years. For *V. cardui*, it is assumed that heavy rainfalls in the Middle East in winter 2018/2019 led to strong reproduction. This apparently resulted in a mass-migration to Europe, and hence the frequent occurrence of this migrant butterfly in many parts of Germany (Hawkes et al. 2022). However, most other species apparently suffered from the severe drought in spring and summer 2019. This was even exacerbated by the previous extremely dry and hot year 2018, which led to significant population declines of various butterfly species across Germany (Richter et al. 2018). The strong fluctuations in butterfly abundance, which are also supported by our data, clearly underline the importance of long-term monitoring for this species group, in order to obtain reliable information on the long-term population development (Sanderson et al. 2021).

Species community structure

The butterfly fauna of the Oettinger Forest is comparatively diverse if compared with other forested areas in Central Europe. Most of these forests are rather dark and dense and thus do not provide suitable ecological niches for most arthropods (Schiess & Schiess-Bühler 1997). In contrast, the Oettinger Forest consists of partly sparse and hence sunny deciduous, mixed and coniferous forests of different succession stages, meadows within the forest and at its edges as well as stony and sunny sites (such as abandoned quarries and sand pits). Such habitat heterogeneity, with many sunny and scarcely vegetated spots, is the essential prerequisite for high species diversity (Kunz 2016, Widmer et al. 2021) that so far has been largely preserved in our study area. The data obtained for the Oettinger Forest underline the high nature conservation value of extensively used ecosystems, such as sustainably used forests as well as habitat mosaics (Thomas 2016).

However, comparing the species compositions of the different years reveals a decrease of the proportion of specialised species of structured open land. Now, the community is more dominated by few habitat generalists, a frequently observed phenomenon (Habel et al. 2016a, 2022). The changes in species composition and especially in their trait composition well reflect the changes after the heavy storms of the late 1990s. Large parts of the spruce forests had been destroyed by these storms. In 2001, large parts of the study area therefore were dominated by wind-blows, exhibiting a structured open land character. This clearly promoted species specialised for such habitats, including numerous taxa that generally suffer from population decline in Central Europe (see also Reinhardt et al. 2020). Over the last 20 years, however, young spruce forest has largely re-established itself on these wind-blow areas. This might explain why numerous species of structured open landscapes have either significantly decreased in abundance or even have not been detected any longer. The negative trend for species of structured open habitats was also reinforced by the fact that other valuable habitats, such as the open quarries and sand pits, have largely lost their open character in the majority of cases. In return, however, some other species have clearly benefited from the sparse forest ecosystem. This underlines the value of the Oettinger Forest as a high-quality forest habitat.

While the total number of species has remained largely constant and abundances have fluctuated strongly, the trait composition of the butterfly community has also clearly shifted. Along our study period, the dominance of few generalists has increased, and specialised species of the forest edge ecotone have decreased. This is also reflected in decreasing Eveness. Such a homogenisation has been observed in many areas of Central Europe in recent decades (Habel et al. 2019b). This may be due to stronger reaction of specialised species to changes in habitat structures (e.g. loss of small-scale high-quality sites) and the availability of specific resources (e.g. larval food plants). The loss of such small-scale structures in the Oettinger Forest has led, for example, to the disappearance of *Cupido minumus*. This species was numerous in 2001 at two strong stands of its exclusive larval food plant *Anthyllis vulneraria* in two old quarries, where it was no longer found in the two later surveys. The reforestation of the wind-blow areas from 2001 has also led to a significant decline or complete disappearance of species of structured open landscapes and forest edge ecotones (e.g. *Boloria dia*, *Coenonympha arcania*).

Overall, the dispersal potential of butterfly species has increased, a phenomenon often observed due to the fragmentation of landscapes and the resulting isolation of habitats (Thomas 2016).

Conclusions

Our study shows that overall species diversity can be maintained in sufficiently large sustainably managed habitat complexes. Our results also show that special sites, such as abandoned quarries, are of very high value for species conservation and overall diversity. Therefore, they should be kept open through appropriate management, otherwise several specialised species faithful to such sites will be at an elevated risk of extinction. Obviously, however, little dispersive habitat specialists are declining, even in large habitat complexes, such as the Oettinger Forest, where flower-rich road-sides are important and efficient dispersal corridors. This might partly be due to natural succession, but also to additional nitrogen inputs from the neighbouring, more intensively used agricultural areas.

A diversity of different habitat structures, including larger open areas with natural dynamics and also anthropogenic interventions (clearing areas, forest meadows), might therefore represent the best strategy for maintaining a high butterfly diversity in Central European forest ecosystems.

Conflict of interest

The authors declare that they have no conflict of interest.

References

Anthes N., Fartmann T., Hermann G., 2008. The Duke of Burgundy butterfly and its dukedom: larval niche variation in Hamearis lucina across Central Europe. Journal of Insect Conservation, 12: 3–14.

Barkmann F., Huemer P., Tappeiner U., Tasser E., Rüdisser J., 2023. Standardized butterfly surveys: comparing transect counts and area-time counts in insect monitoring. Biodiversity and Conservation, 32: 987–1004. https://doi.org/10.1007/s10531-022-02534-2

Benjamini Y., Hochberg Y., 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (Methodological), 57: 289–300.

Bink F.A., 1992. Ecologische atlas van de dagvlinders van Noordwest-Europa. Schuyt, Haarlem, 512 p.

Bonelli S., Cerrato C., Barbero F., Boiani M.V., Buffa G., Casacci L.P., Fracastoro L., Provenzale A., Rivella E, Zaccagno M., Balletto E., 2021. Changes in alpine butterfly communities during the last 40 years. Insects, 13: 43. https://doi.org/10.3390/insects13010043

Bowler D.E., Heldbjerg H., Fox A.D., Jong M., Böhning-Gaese K., 2019. Long-term declines of European insectivorous bird populations and potential causes. Conservation Biology, 33: 1120–1130. https://doi.org/10.1111/cobi.13307

Cardoso P., Barton P.S., Birkhofer K., Chichorro F., Deacon C., Fartmann T., Fukushima C.S., Gaigher R., Habel J.C., Hallmann C.A., Hill M.J., Hochkirch A., Kwak M.L., Mammola S., Ari Noriega J., Orfinger A.B., Pedraza F., Pryke J.S., Roque F.O., Settele J., Simaika J.P., Stork N.E., Suhling F., Vorster C., Samways M.J., 2020. Scientists' warning to humanity on insect extinctions. Biological Conservation, 242: 108426. https://doi.org/10.1016/j.biocon.2020.108426

Dennis R.L.H., Eales H.T., 1997. Patch occupancy in *Coenonympha tullia* (Muller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. Journal of Insect Conservation, 1: 167–176. https://doi.org/10.1023/A:1018455714879

Ebert G. (ed.), 1994. Die Schmetterlinge Baden-Württembergs. E. Ulmer, Stuttgart, 518.

Ganuza C., Redlich S., Uhler J., Tobisch C., Rojas-Botero S., Peters M.K., Zhang J., Benjamin C.S., Englmeier J., Ewald J., Fricke U., Haensel M., Kollmann J., Riebl R., Uphus L., Müller J., Steffan-Dewenter I., 2022. Interactive effects of climate and land use on pollinator diversity differ among taxa and scales. Science Advances, 8, eabm9359. https://doi.org/10.1126/sciadv.abm9359

Habel J.C., Samways M.J., Schmitt T., 2019a. Mitigating the precipitous decline of terrestrial European insects: Requirements for a new strategy. Biodiversity and Conservation, 28: 1343–1360. https://doi.org/10.1007/s10531-019-01741-8

Habel J.C., Schmitt T., Gros P., Ulrich W., 2022. Breakpoints in butterfly decline in Central Europe over the last century. Science of The Total Environment, 851: 158315. https://doi.org/10.1016/j.scitotenv.2022.158315

Habel J.C., Segerer A., Ulrich W., Torchyk O., Weisser W.W., Schmitt T., 2016. Butterfly community shifts over two centuries: Shifts in butterfly communities. Conservation Biology, 30: 754–762. https://doi.org/10.1111/cobi.12656

Habel J.C., Trusch R., Schmitt T., Ochse M., Ulrich W., 2019b. Long-term large-scale decline in relative abundances of butterfly and burnet moth species across south-western Germany. Scientific Reports, 9: 14921. https://doi.org/10.1038/s41598-019-51424-1

Hallmann C.A., Sorg M., Jongejans E., Siepel H., Hofland N., Schwan H., Stenmans W., Müller A., Sumser H., Hörren T., Goulson D., de Kroon H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE, 12: e0185809. https://doi.org/10.1371/journal.pone.0185809

Hallmann C.A., Ssymank A., Sorg M., de Kroon H., Jongejans E., 2021. Insect biomass decline scaled to species diversity: General patterns derived from a hoverfly community. Proceedings of the National Academy of Science U.S.A., 118: e2002554117. https://doi.org/10.1073/pnas.2002554117

Hammer Ø., Harper D.A.T., Ryan P.D., 2001. PAST: Paleontological StatisticsSoftware Package for Education and Data Analysis. Palaeontologia Electronica, 4: 4.

Harrison J.G., Shapiro A.M., Espeset A.E., Nice C.C., Jahner J.P., Forister M.L., 2015. Species with more volatile population dynamics are differentially impacted by weather. Biology Letters, 11: 20140792. https://doi.org/10.1098/rsbl.2014.0792

Hausmann A., Ulrich W., Segerer A.H., Greifenstein T., Knubben J., Morinière J., Bozicevic V., Doczkal D., Günter A., Müller J., Habel J.C., 2022. Fluctuating insect diversity, abundance and biomass across agricultural landscapes. Scientific Reports, 12: 17706. https://doi.org/10.1038/s41598-022-20989-9

Hawkes W.L.S., Walliker E., Gao B., Forster O., Lacey K., Doyle T., Massy R., Roberts N.W., Reynolds D.R., Özden Ö., Chapman J.W., Wotton K.R., 2022. Huge spring migrations of insects from the Middle East to Europe: quantifying the migratory assemblage and ecosystem services. Ecography, 10: e06288. https://doi.org/10.1111/ecog.06288

Huemer P., Tarmann G., 2001. Artenvielfalt und Bewirtschaftungsintensität: Probelamanalyse am Beispiel der Schmetterlinge auf Wiesen und Weiden Südtirols. Gredleriana, 1: 331–418.

Kadlec T., Tropek R., Konvicka M., 2012. Timed surveys and transect walks as comparable methods for monitoring butterflies in small plots. Journal of Insect Conservation, 16: 275–280. https://doi.org/10.1007/s10841-011-9414-7

Kral-O'Brien K.C., Antonsen A.K., Hovick T.J., Limb R.F., Harmon J.P., 2021. Getting the most from surveys:

How method selection and method modification impact butterfly survey data. Annals of the Entomological Society of America, 114: 719–726. https://doi.org/10.1093/aesa/saab004

Kunz, W., 2016. Species conservation in managed habitats: The myth of a pristine nature. Wiley-VCH, Weinheim, 293 p.

Leroy B.M.L., Seibold S., Morinière J., Bozicevic V., Jaworek J., Roth N., Vogel S., Zytynska S., Petercord R., Eichel P., Weisser W.W., 2022. Metabarcoding of canopy arthropods reveals negative impacts of forestry insecticides on community structure across multiple taxa. Journal of Applied Ecology, 59: 997–1012. https://doi.org/10.1111/1365-2664.14110

Lin B.-L., Kumon Y., Inoue K., Tobari N., Xue M., Tsunemi K., Terada A., 2021. Increased nitrogen deposition contributes to plant biodiversity loss in Japan: Insights from long-term historical monitoring data. Environmental Pollution, 290: 118033. https://doi.org/10.1016/j.envpol.2021.118033

Melbourne B.A., Hastings A., 2008. Extinction risk depends strongly on factors contributing to stochasticity. Nature, 454: 100–103. https://doi.org/10.1038/nature06922

Mills S.C., Oliver T.H., Bradbury R.B., Gregory R.D., Brereton T., Kühn E., Kuussaari M., Musche, M., Roy D.B., Schmucki R., Stefanescu C., van Swaay, C., Evans, K. L., 2017. European butterfly populations vary in sensitivity to weather across their geographical ranges. Global Ecology and Biogeography, 26: 1374–1385. https://doi.org/10.1111/geb.12659

Møller A.P., 2019. Parallel declines in abundance of insects and insectivorous birds in Denmark over 22 years. Ecology and Evolution, 9: 6581–6587. https://doi.org/10.1002/ece3.5236

Müller J., Brandl R., Brändle M., Förster B., de Araujo B.C., Gossner M.M., Ladas A., Wagner M., Maraun M., Schall P., Schmidt S., Heurich M., Thorn S., Seibold S., 2018. LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos, 127: 814–824. https://doi.org/10.1111/oik.04972

Olden J.D., 2006. Biotic homogenization: a new research agenda for conservation biogeography. Journal of Biogeography, 33: 2027–2039. https://doi.org/10.1111/j.1365-2699.2006.01572.x

Pickett S.T., White P.S., 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Fla., 472 p.

Pykälä J., 2000. Mitigating Human Effects on European Biodiversity through Traditional Animal Husbandry. Conservation Biology, 14: 705–712. https://doi.org/10.1046/j.1523-1739.2000.99119.x

Raven P.H., Wagner D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. Proceedings of the National Academy of Science U.S.A., 118: e2002548117. https://doi.org/10.1073/pnas.2002548117

Reinhardt R., Harpke A., Caspari S., Dolek M., Kühn E., Musche M., Trusch R., Wiemers M., Settele J., 2020. Verbreitungsatlas der Tagfalter und Widderchen Deutschlands. Ulmer, Stuttgart, 428 p.

Richter A., Hauck J., Feldmann R., Kühn E., Harpke A., Hirneisen N., Mahla A., Settele J., Bonn A., 2018. The social fabric of citizen science—drivers for long-term engagement in the German butterfly monitoring scheme. Journal of Insect Conservation, 22: 731–743. https://doi.org/10.1007/s10841-018-0097-1

Rumohr Q., Baden C.U., Bergtold M., Marx M.T., Oellers J., Schade M., Toschki A., Maus C., 2023. Drivers and pressures behind insect decline in Central and Western Europe based on long-term monitoring data. PLoS One, 18: e0289565. https://doi.org/10.1371/journal.pone.0289565

Sánchez-Bayo F., Wyckhuys K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation, 232: 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Sanderson C., Braby M.F., Bond S., 2021. Butterflies Australia: a national citizen science database for monitoring changes in the distribution and abundance of Australian butterflies. Austral Entomology, 60: 111–127. https://doi.org/10.1111/aen.12513

Schiess H., Schiess-Bühler C., 1997. Dominanzminderung als ökologisches Prinzip: eine Neubewertung der ursprünglichen Waldnutzungen für den Arten- und Biotopschutz am Beispiel der Tagfalterfauna eines Auenwaldes in der Nordschweiz. Mitteilungen der Eidgenössischen Forschungsanstalt für Wald, Schnee und Landschaft, 72: 3–127.

Schmitt T., 2003. Influence of forest and grassland management on the diversity and conservation of butterflies and burnet moths (Lepidoptera, Papilionoidea, Hesperiidae, Zygaenidae). Animal Biodiversity and Conservation, 26.2: 51–67.

Seibold S., Gossner M.M., Simons N.K., Blüthgen N., Müller J., Ambarlı D., Ammer C., Bauhus J., Fischer M., Habel J.C., Linsenmair K.E., Nauss T., Penone C., Prati D., Schall P., Schulze E.-D., Vogt J., Wöllauer S., Weisser W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature, 574: 671–674. https://doi.org/10.1038/s41586-019-1684-3

Sparks T.H., Greatorex-Davies J.N., Mountford J.O., Hall M.L., Marrs R.H., 1996. The effects of shade on the plant communities of rides in plantation woodland and implications for butterfly conservation. Forest Ecology and Management, 80: 197–207.

Stefanescu C., Askew R.R., Corbera J., Shaw R.M., 2012. Parasitism and migration in southern Palaearctic populations of the painted lady butterfly, *Vanessa cardui* (Lepidoptera: Nymphalidae). European Journal of Entomology, 109: 85–94.

Suman A., Ravikanthachari N., Kunte K., 2021. A comparison between time-constrained counts and line transects as methods to estimate butterfly diversity and monitor populations in tropical habitats (preprint). BioRxiv, 2021, 2021.09.04.458959.

Ternisien M., Deschamps-Cottin M., Lizée M.H., March L., Robles C., Vila B., 2023. How butterfly communities are structured and have changed in urbanized areas of Marseille: a 12-year monitoring survey. Urban Ecosystems, 26: 1427–1438. https://doi.org/10.1007/s11252-023-01377-1

Thomas J.A., 2016. Butterfly communities under threat. Science, 353: 216–218. https://doi.org/10.1126/science.aaf8838

Van Dyck H., Van Strien A.J., Maes D., Van Swaay C.A.M., 2009. Declines in common, widespread butterflies in a landscape under intense human use. Conservation Biology, 23: 957–965. https://doi.org/10.1111/j.1523-1739.2009.01175.x

Viljur M.-L., Teder T., 2016. Butterflies take advantage of contemporary forestry: Clear-cuts as temporary grasslands. Forest Ecology and Management, 376: 118–125. https://doi.org/10.1016/j.foreco.2016.06.002

Voith, J., 2016. Rote Liste gefährdeter Tiere Bayerns – Grundlagen. 4. Fassung. Bayerisches Landesamt für Umwelt, München, 11 p.

Wagner D.L., 2020. Insect Declines in the Anthropocene. Annual Review of Entomology, 65: 457–480. https://doi.org/10.1146/annurev-ento-011019-025151

Walker L.R., del Moral R., 2003. Primary succession and ecosystem rehabilitation. Cambridge University Press, Cambridge, 458 p.

Warren M.S., Maes D., van Swaay C.A.M., Goffart P., Van Dyck H., Bourn N.A.D., Wynhoff I., Hoare D., Ellis S., 2021. The decline of butterflies in Europe: Problems, significance, and possible solutions. Proceedings of the National Academy of Science U.S.A., 118: e2002551117. https://doi.org/10.1073/pnas.2002551117

Widmer I., Mühlethaler R., Baur B., Gonseth Y., Guntern J., Klaus G., Knop E., Lachat T., Moretti M., Pauli D., Pellissier L., Sattler T., Altermatt F., 2021. Insektenvielfalt in der Schweiz: Bedeutung, Trends, Handlungsoptionen. Swiss Academies Reports, 16: 9. https://doi.org/10.5281/ZENODO.5144739

Wiemers M., Balletto E., Dincă V., Fric Z.F., Lamas G., Lukhtanov V., Munguira M.L., van Swaay C.A.M., Vila R., Vliegenthart A., Wahlberg N., Verovnik R., 2018. An updated checklist of the European Butterflies (Lepidoptera, Papilionoidea). ZooKeys, 811: 9–45. https://doi.org/10.3897/zookeys.811.28712